Effect of mowing, rust infection and seed production upon C and N reserves and morphology of the perennial Veratrum album L. (Liliales, Melanthiaceae)

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Effect of mowing, rust infection and seed production upon C and N reserves and morphology of the perennial *Veratrum album* L. (Liliales, Melanthiaceae)

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Abstract

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In this field study the effect of mowing, rust infection and seed production was determined on nonstructural carbohydrate (C) and Kjeldahl nitrogen (N) reserves in rhizomes, as well as on plant morphology of the perennial weed *Veratrum album* L. (Liliales, Melanthiaceae). Rust infection and seed production had only a minimal influence on the concentrations of C and of N during either the summer or the following winter. However, mowing one month after early shoot growth led to decreased C (−40%) and increased N (+100%) concentrations of rhizomes sampled during the following winter. In a long-term experiment, the decrease in C reserves was shown to coincide with dwarfism of *V. album* plants. Mowing for six consecutive years reduced total plant biomass by 50%. Accordingly, total N and C reserves per plant rhizome decrease substantially. However, seasonal patterns of C and N concentrations were not influenced by mowing, except for the differences in winter concentrations that were already observed in the short-term experiment. Long-time mowing not only led to dwarfism of *V. album* plants, but also significantly decreased generative and vegetative proliferation.

Key words: Veratrum album – Nitrogen/carbohydrate reserves – Mowing – Seed production – Fungal infection.

Introduction

Assessment of the impact of stress factors on plant fitness and vigour is a crucial factor when determining strategies for weed control. This is particularly problematical for perennial weeds because the fitness component 'seed production' is very difficult to assess. *Veratrum album* L. is a long-lived pasture weed with rhizomes being fully grown after 40 years (Hess et al. 1967). On mountain grassland, *V. album* causes two main problems: first, it can locally reach a cover of up to 80%, causing yield losses of 40% of dry weight (Troxler and Rouel 1987). Secondly, this alkaloid-containing plant is toxic to cattle, causing severe intestinal problems and embryonic deformations (Binns et al. 1972). For these reasons extended work has been devoted to the chemical, mechanical and biological control of *V. album* (Troxler and Rouel 1987; Dorée 1988; Milevoj 1988; Schaffner 1994). As attempts to control this long-lived weed rarely lead to the death of individual plants, survival rate is not a suitable indicator of stress. In this study, we investigated the effect of mowing, rust infection and seed production within one season (short-term stress), as well as mowing for several consecutive years (long-term stress), on Kjeldahl nitrogen and nonstructural carbohydrate reserves, and on the morphological appearance of *V. album*.

Materials and methods

Experimental species

V. album (Liliales, Melanthiaceae) is a perennial monocot native to Europe and Asia. In central Europe, it was originally found in the dwarf scrub zone and open grassland above the timberline, from where it has expanded its range to pastures above approximately 800 m a.s.l. The most vigorous individuals occur on nutrient-rich soils. *V. album* overwinters as a large rhizome with a preformed bud which contains the leaves that will develop during the following growing season. The vertical rhizomes can reach a length of 15 cm and a diameter of 6 cm. At about 1000 m, the buds do not emerge before late April. With up to 15 leaves of 15–40 × 10–20 cm size, *V. album* produces a large amount of above ground biomass. Flowering, which occurs about every three to four years, starts in late June. In September, the green parts wither and collapse while stems with dry fruit stay upright until the first snow arrives. *V. album* reproduces both vegetatively and by seeds. Vegetative reproduction is generally initiated after flower formation.

Plant analysis

The study was conducted between 1991 and 1993 on two pastures, named 'Vieille Môle' and 'Perotte', in the Swiss Jura (Chasseral, Bern; 47°07′ N/7°00′ E). The site facing north-eastern at Vieille Môle, 1000 m a.s.l., is an open, moist pasture surrounded by a streamlet, a small forest and by more intensively managed pastureland. Perotte is 5 km north of Vieille Môle on a north-facing hillside at an elevation of 1050 m a.s.l. The study site is part of an extensive pasture which is interspersed with solitary spruce trees.

At Vieille Môle, the first buds emerged between 20–26 April, about one week earlier than at Perotte. Within two weeks, all buds had emerged. In both places plants were cut in early June, i.e. about one month after early shoot growth, 5 cm above ground level so that foliage was, more or less, completely removed. Mown *V. album* plants never regenerate above-ground organs within the same season.

The short-term study was carried out in 1991 at Vieille Môle. On 3 June, some 50 randomly chosen plants were mown and labelled. On 26 June, samples were collected of mown plants (M), of plants which started flowering (F), of plants which showed first signs of rust infection (I), and of non-flowering control plants (Co). In 1991, some *V. album* plants at Vieille Môle were heavily infected by the foliar pathogen *Puccinia veratri* Duby. This heteroecious rust fungus infects *V. album* in the dikaryotic phase. On 26 November, the sampling procedure was repeated. For group c) and d), only those plants were selected which were heavily infested by the rust during the vegetative period, or free of visible infection, respectively.

The long-term study was performed at Perotte. Plants of one part of the homogenous pasture were mown every year between 1987 and 1990 by the farmer, and in 1991/1992 by one of us (U.S.).

On 6 June 1992, some 100 plants which had been mown for six consecutive years were labelled and not mown any more. The other plants of this part of the pasture were mown for the seventh consecutive time. Plants of the unmown part of the pasture were used as controls. On 8 June, 2 September, 30 November 1992, 17 May and 29 June 1993, samples were collected of plants which had been mown for seven consecutive years (7′), of plants which had been mown for six consecutive years but were not harvested during the investigation period (6′), and of control plants.

For each analysis group, 6–8 (Vieille Môle) and 8–10 (Perotte) plants were randomly chosen. Care was taken to sample plants with only one shoot per rhizome. Following collection, samples were washed, weighed, dried at 70 °C for 24 h, and weighed again. From all rhizomes, a 30 mm long rooted part beginning near the apex was chopped into small pieces, immersed in liquid nitrogen and pulverized in a dismembrator (Braun, Melsungen, Germany). Total nitrogen of the powder was determined after wet digestion according Kjeldahl at 335 °C with modified sulphuric acid (Bohley 1967). For determination of nonstructural carbohydrates (fructosans and sugars), samples were extracted at 95–100 °C with water (pH 8) for 20 min, and then centrifuged. One ml of the supernatant was added to 1 ml 0.2 M HCl and hydrolyzed at 95–100 °C for 10 min. Nonstructural carbohydrates were determined photometrically, using fructose as a standard (Schnyder and Nelson 1987, modified). For analysis of Kjeldahl nitrogen (N) and nonstructural carbohydrates (C), two parallel samples of 50 mg were analyzed per rhizome.

Results

Impact of mowing, fungal infection and seed production on C and N reserves within a season

Rust infection and flowering did not affect concentrations of C and N in the rhizomes compared to control plants, neither during summer nor in the following winter (Fig. 1). Only the C:N ratio of infected plants was slightly enhanced during summer ($P<0.1$; Mann-Withney U-test) but reached the same level as the control plants in winter again. In contrast, mowing considerably changed C and N concentrations of rhizomes. In winter, the C and N concentrations were 40% lower and 100% higher, respectively, than in control plants.

These findings suggest that mowing may have considerable impact on the vigour of *V. album* plants. We inferred that mowing for several consecutive years should lead to a depletion of C reserves in rhizomes and to a subsequent reduction in above-ground growth.

Impact of repeated mowing on morphology and population density

Between 1990 and 1993, densities of both the mown (2.3–2.2 individuals/m^2) and the unmown subpopulation (4.3–4.5 individuals/m^2) remained constant. During this period, only three plants of the mown subpopulation died. Although plant density was not affected, mowing for 6 consecutive years led to a noticeable dwarfism of *V. album* plants. Shoot length of plants obtained from that part of the pasture which had been mown for the six previous years was approximately 30% less than that of control plants (Fig. 2). Dry weight of both above- and below-ground biomass decreased to about 50% (Table 1). One undisturbed season was not sufficient for mown plants to regain control plant size.

The mean relative portion of total dry matter allocated to the different vegetative plant organs did not differ between mown and control plants. However, *V. album* plants mown for several consecutive years have not been observed to flower. Since vegetative proliferation generally is initiated in the season which follows flower formation, mowing seems to have a drastic effect in total reproduction of *V. album*.

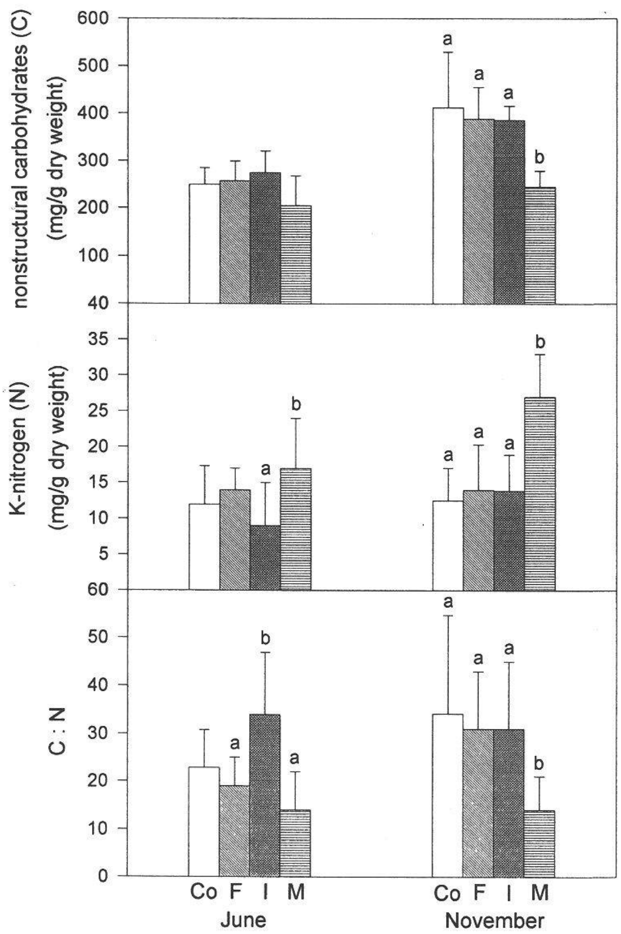

Fig. 1. Effect of mowing (M), flowering (F) and fungal infection (I) of *Veratrum album* upon concentration of nonstructural carbohydrates (C) and Kjeldahl nitrogen (N), as well as C:N ratio of rhizomes in summer (26 June 1991) and winter (26 November 1991). Co are control plants. Data are means of 6–8 replicates ± standard deviation. Within each group, bars indicated by ‘a’ differ significantly from bars indicated by ‘b’ ($P<0.05$; Mann-Withney U-test).

Effect of repeated mowing on C and N contents of rhizomes

Seasonal changes in concentration and content of C and N of control plants and treated plants are shown in Fig. 3. Due to the larger rhizomes, C and N contents per plant rhizome were much higher in control plants than in mown plants. However, concentrations differed significantly only in winter. As found in the short-term experiment, plants mown during the study period had lower C ($P<0.01$; Mann-Withney U-test) and higher N concentrations ($P<0.05$; Mann-Withney U-test) during winter than control plants. Since the C concentrations of mown and control plants were at the same low level during early shoot growth, relative investment of stored C in spring growth was considerably larger in control plants (Fig. 3).

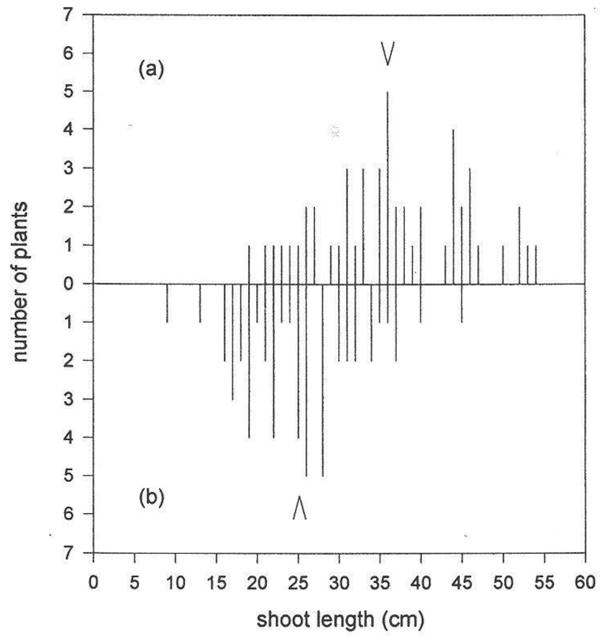

Fig. 2. Shoot length of *Veratrum album* plants which had never been mown (a), compared to plants which had been mown for 6 consecutive years (b). The arrows indicate the median of both groups. Measurements were taken from 50 randomly sampled plants each, on 8 July 1992 at Perotte.

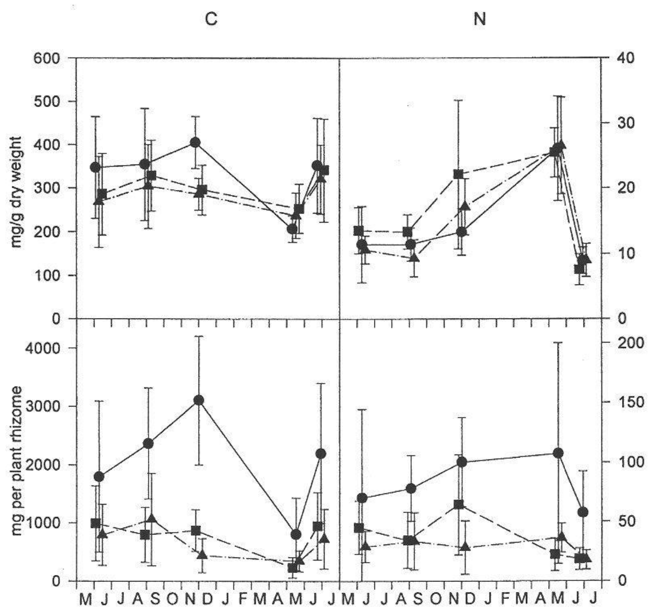

Fig. 3. Seasonal patterns of contents and concentrations of C and N of rhizomes of *Veratrum album*. Measurements were taken from plants which had been mown for 7 consecutive years (■), from plants which had been mown for six consecutive years but were not harvested during the investigation period (▲), and from control plants (●). Data are means of 8–10 replicates ± standard deviation. Main period of above-ground growth in spring is between mid May and early June.

Table 1. Total amount (g), and relative portions (in brackets), of dry matter allocated to different organs of *Veratrum album* plants which had been mown for seven consecutive years (7′), of plants which had been mown for 6 consecutive years but were not harvested during the investigation period (6′), and of control plants at the end of the investigation period (29 June 1993) at Perotte. Data are means of n replicates ± standard deviation.

	Control	6′	7′
n	9	8	10
Rhizomes	6.21±2.95 (15.4%)	2.96±2.17 (13.9%)	2.67±1.36 (15.5%)
Roots	14.87±4.04 (36.9%)	8.18±1.94 (38.5%)	6.83±1.94 (39.6%)
Leaves	11.25±2.52 (27.9%)	6.24±1.36 (29.4%)	4.64±1.71 (26.9%)
Shoot	7.98±4.48 (19.8%)	3.86±0.99 (18.2%)	3.12±1.39 (18.1%)

Discussion

The importance of reserves in supporting seed production varies considerably among plant species (Chapin et al. 1990). In the long-lived *V. album*, reserves of flowering and non-flowering plants differed neither at the beginning of the flowering period nor in the following winter. These findings are consistent with other studies in which a decline in C reserves by reproduction was not detectable in long-lived plants (Mark and Chapin 1988; Horvitz and Schemske 1988). Also, rust infection under natural conditions did not cause substantial changes in C and N reserves. Only during the summer did plants infected by *Puccinia veratri* show signs of N loss. The low effect of rust infection on C an N reserves in rhizomes in this study may be due to the fact that during the investigation period infestation reached its maximum only in late summer. A release of large doses of fungal inoculum already in spring to create a fast and high level of epidemic may have more effect on C and N reserves of the rhizomes.

In the long-term mowing experiment, N and C concentrations differed between stressed plants and control plants during winter, but not during the vegetative period. The temporary accumulation of N after removing the above-ground organs. may be explained by the interruption of N export from rhizomes to shoots and possible continued N accumulation by roots. The lower C concentrations in the rhizomes of mown plants during winter were to be expected considering the lack of assimilative organs throughout the summer. In spite of the considerable difference during winter, C concentrations in rhizomes of mown plants in spring were at level with those of control plants again. These findings suggested that *V. album* acclimatizes to stress by investing less reserves in spring growth, leading in the long-term to a decrease in overall plant size, and by temporarily ceasing sexual reproduction. For the long-lived *V. album*, it may be more important to survive periods of stress than to invest all remaining reserves in reproduction. Sexual reproduction is generally believed to be a high-risk investment (Bloom et al. 1985).

In the analysis of the carbohydrate patterns of several alpine plant species, Mooney and Billings (1960) found that early shoot growth utilizes considerable quantities of carbon reserves. After this period, a rapid accumulation of the reserves in rhizomes and roots was observed. The carbohydrate pattern in the rhizomes of *V. album* seems to behave quite similar. The analysis of the annual carbohydrate pattern of healthy *V. album* plants indicates that the nonstructural carbohydrate pool in the rhizomes was refilled to a considerable extent at the time when the plants were mown, i.e. one month after early shoot growth (Fig. 3). It would be of interest to investigate the effect of mowing at a time when the carbohydrate reserves in the rhizomes are still at a low level.

In summary, our study provides evidence that mowing one month after early shoot growth for several years results in dwarfism of *V. album* plants, but that long-time mowing had no effect on C and N concentrations of rhizomes during the vegetative period, or on the allocation of dry matter to plant organs. Moreover, survival of mown plants was not reduced during the period of investigation. Nevertheless, mowing seems to have considerable impact on the fitness of *V. album* plants, since plants mown for several consecutive years stopped flowering. Further investigations will be necessary to elucidate the functional links between these findings.

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References

Binns W., Keeler R. F. and Balls L. D. 1972. Congenital deformities in lambs, calves and goats resulting from maternal ingestion of *Veratrum californicum:* hare clip, cleft palate, ataxia and hypoplasia of metacarpal and metatarsal bones. Clinical Toxicol. 5: 245–261.

Bloom A. J., Chapin F. S. and Mooney H. A. 1985. Resource limitation in plants – an economic analogy. Annu. Rev. Ecol. Syst. 16: 363–392.

Bohley P. 1967. Reihenbestimmungen von Stickstoff im Ultramikromaßstab. Hoppe Seyler's Z. Physiol. Chem. 348: 100–110.

Chapin F. S., Schulze E.-D. and Mooney H. A. 1990. The ecology and economics of storage in plants. Annu. Rev. Ecol. Syst. 21: 423–447.

Dorée A. 1988. Le vératre ou elebore blanc. CEMAGREF-INERM (Grenoble). 5e réunion FAO des herbages de montagne. Bled, Yougoslavie.

Hess H. E., Landolt E. and Hirzel R. 1967. Flora der Schweiz 3. Birkhäuser, Basel.

Horvitz C. C. and Schemske D. W. 1988. Demographic cost of reproduction in a neotropical herb: an experimental field study. Ecology 69: 1741–1745.

Mark A. F. and Chapin F. S. 1988. Seasonal control over allocation to reproduction in a tussock-forming and a rhizomatous species of *Eriophorum* in central Alaska. Oecologia 78: 27–34.

Milevoj L. 1988. Weed control problems in intensively managed pastures in Slovenia. Fragmenta Herbologica Jugoslavica 17: 123–131.

Mooney H. A. and Billings W. D. 1960. The annual carbohydrate cycle of alpine plants as related to growth. Amer. J. Bot. 47: 594–598.

Schaffner U. 1994. Interactions between *Veratrum album* L. and its herbivores: prospects of biological control of this native weed. PhD thesis, Zoological Institute, University of Bern, Switzerland.

Schnyder H. and Nelson C. J 1987. Growth rates and carbohydrate fluxes within the elongation zone of tall fescue leaf blades. Plant Physiol. 85: 548–553.

Troxler J. and Rouel M. 1987. Possibilités de lutte contre le vératre. 5e réunion FAO des herbages de montagne. Bled, Yougoslavie.